

On the Relation of Imperfect Functioning of the  
Testis to Imperfect Descent.

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ON the RELATION of IMPERFECT FUNCTIONING of the TESTIS to  
IMPERFECT DESCENT.

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" . . . there remain many unsolved problems. Take as an instance the descent of the testes in the Mammalia. Neither direct nor indirect equilibration accounts for this. We can not consider it an adaptive change, since there seems no way in which the production of sperm-cells, internally carried on in a bird, is made external by adjustment to the changed requirements of mammalian life. Nor can we ascribe it to survival of the fittest; for it is incredible that any mammal was over advantaged in the struggle for life by this changed position of these organs. Contrariwise, the removal of them from a place of safety to a place of danger would seem to be negated by natural selection. Nor can we regard the transposition as a concomitant of re-equilibration, since it can hardly be due to some change in the general physiological balance."  
HERBERT SPENCER. Principles of Biology. 1880. v.1. p. 573.

In all Vertebrates the testes are developed in contact with the ventral surface of the kidneys, behind the peritoneum covering the body-cavity. In some they remain permanently in this situation, but it is characteristic of the majority of Mammals that in the course of development they leave their primitive lodgment and migrate posteriorly and ventrally to the terminal periphery where they protrude at the surface of the body-wall. This protrusion constitutes the scrotum and varies in character from that of a pair of small ill-defined slightly elevated areas to that of a capacious definite pedunculated sac.

A survey of the Vertebrates will show that the testes in different cases are to be found in one or other of the following situations : -

- A. Permanently intra-abdominal.
1. In the primitive position.
  2. Close to, but a little lateral or caudad to the situation of the primitive kidneys.
  3. In the inguinal region in close approximation to the ventral abdominal wall.
- B. Permanently extra-abdominal.
1. Subintegumental in the inguinal or perineal regions.
  2. Within an indefinite sessile scrotum.
  3. Within a definite and pendulous scrotum.
- C. Periodically intra- and extra-abdominal.

These mammals in which the testes remain permanently abdominal are grouped as the testiconda.

The following table shows the position of the testes in the various groups : -

/ Table.

CLASS.	SUBCLASS.	ORDER.	SUB-ORDER.	
Pisces. Amphibia. Reptilia. Aves.				In the primitive position.
Mammalia.	Prototheria.	Monotrema.		The only example in mammals of these organs anterior to the kidneys.
	Metatheria.	Marsupalia.		In an external prepenial peduncula - :ted scrotum.
	Eutheria.	Edentata.	Bradypodidae. ) Myrmecophagidae ) Dasypodidae. Manidae. Crycteropodidae.	Close to each other lying on the rec- :tum between it and the bladder. Lying above brim of pelvis. In the inguinal canal. Inguinal, but they appear to descend at all events temporarily, into a scrotum.
		Sirenia. Cetacea. Rodentia.		In the primitive position. do. The testes in the rutting season form projections in the groins but (except in Duplicidentata) do not completely leave the cavity of the abdomen. Lying immediately caudad to the kid - :neys.
		Insectivora.	Centetinae.  Chrysochloris Oryzorictinae. Erinaceinae	do. Lying near the urethra. On the under side of the inguinal canal.
			Soricidae. ) Macroscelidae. ) Solenodontidae.	Project at the periphery of the pe - :rineum. Received into perineal pouches.
		Chiroptera.		In, or close to the primitive positi - :on, or subintegumental in the ingui - :nal or perineal regions.
		Ungulata.	Proboscoidea. Hyracoidea. Perissodactyla.	Below or behind the kidneys. do. In an external pedunculated scrotum (except Rhinocerus and Tapir in which the testes remain in the abdo - :minal cavity.
		Carnivora.	Artiodactyla. Pinnipedia.	In an external pedunculated scrotum.
			Phocidae.	In inguinal region in close approxi - :mation to the abdominal wall.
			Otariidae.	In external scrotum.
		Primates.	Fissipedia. Lemuroidea.	In an external pedunculated scrotum. In lower forms - in sessile scrotum. In the higher - in an external pedun - :culated scrotum.
			Anthropoidea.	In an external pedunculated scrotum.



A review of the above leads to certain well-founded conclusions. It is seen that the different positions in which the testis is found are merely stages in a migration from the primitive position near the kidneys to a peripheral external pendunculated scrotum. It is seen also that a peripheral position of the testis is characteristic of the more impulsively active mammals.

The migration has been most thoroughly studied in the human subject and provides a very complete example of the manner in which ontogeny repeats and condenses phylogeny in whole or part; of the manner in which the development of the organs and their functions in man repeats and condenses in time and stages the parts of the various organ-ontogenies and their functions necessary to complete the ontogeny of the whole organism. (Müller-Haeckel law.)

In the human, the testis, during the third month of intrauterine life, passes from the primitive position to the iliac fossa; from the fourth to the seventh months it lies at the site of the internal abdominal ring in the inguinal region; during the seventh month it passes through the ventral abdominal wall to reach the external abdominal ring; remaining there during the eighth month it passes after birth to the fundus of the scrotum. But in fully 10 % of all male children born at term the testes are found in the inguinal canal, not having completed the migration. In most cases the testes pass into the scrotum without difficulty during the first weeks of life; in others the condition may persist until spontaneous descent occurs at some time before puberty.

## THE MECHANISM of the MIGRATION.

The structures principally concerned in this process are the testes, the scrotum, and the gubernaculum and its associated tissues.

### THE TESTES.

The great function of the testes is that of spermatogenesis. They also provide the male hormone, in response to which the essentially male secondary sexual characters are exhibited.

"In man and other mammals it has long been recognised that in addition to the germinal cells of the testis there are also present other cells, sometimes called interstitial cells, that, so far as known, have no immediate function in connection with the germ-cells, or at least that have other important functions outside the relation to the reproductive organ. That some internal secretion from these cells has an important influence on the secondary sexual characters rather than anything done by or produced by the germinal cells has been very clearly shown by evidence derived from three separate sources, namely, from the operation known as vasectomy, from an exceptional condition known as cryptorchidism, and more indirectly from X-ray treatment." (MORGAN, p.35)

While there is no actual isolation of the germ-cells, the testes being exposed to all influences which affect the body generally, yet there is distinctly an apartness of the germ-cells, for the testes belong to the race rather than to the individual. The body primarily serves as a mere carrier of these organs which are peculiar in that they do not bear the same relation to the economy of the individual as do the others. The migration of the testes to the periphery for this reason does not disturb the general economy, and just as reproduction itself essentially consists of a separating off of a portion of the organism, so the

essential organs of reproduction become separated, in consequence of their migration, from the viscera which belong entirely to the individual organism.

With the exception of the heart, the testes are the densest organs in the vertebrate organism and are relatively small bodies, compact in form. Each is attached to the mesonephros, or Wolffian body, by a suspensory ligament, the mesorchium, during development. In the adult the testes are suspended in the scrotum by the spermatic cords and as they migrate thereinto they become invested in their course by coverings derived from the serous, muscular, and fibrous layers of the abdominal parietes.

#### THE SCROTUM.

The scrotum is a pouch composed of skin and the dartos tunic and is divided on its surface into two lateral portions by a median raphe which is continued forwards to the under surface of the penis and backwards along the middle line of the perineum to the anus. The skin is very thin, of a brownish colour, and generally thrown into rugae. It is well supplied with sebaceous follicles, the secretion of which has a peculiar odour, and is beset with thinly scattered crisp hairs, the roots of which are visible through the skin.

The dartos tunic is a thin layer of non-striated muscle-fibres, continuous around the base of the scrotum with the two layers of superficial fascia of the groin and of the perineum. It sends inwards a septum which extends between the

median raphe and the under surface of the penis, as far as its root, and divides the scrotum into two cavities for the testes. It is closely applied to the skin externally, and connected with the subjacent parts by a delicate areolar tissue, upon which it glides with the greatest facility. The dartos, in contraction, shortens the scrotum causing corrugation of the skin.

The scrotum is an area of skin specially modified, remarkable in that there is no fat in the subcutaneous areolar tissue. In the fattest of men the scrotum is fat-free, but in a castrate the scrotum is loaded with fat. The butcher's test for prime beasts is the amount of fat therein. KLAATSCH has shown that in many mammals the site of the future scrotum is marked out by a certain area of skin, the area scroti, evident both by its naked-eye and microscopic character. The hairy covering is less marked, the small hairs arise from projections due to elevations of the cutis which possess a thin epidermic covering. Its most characteristic microscopic structure is a layer of unstriped muscle, ceasing at the edge of the area. In the middle line the areae scroti coalesce.

WHITE and MARTIN state that in those cases in which the testis comes to occupy an abnormal position in the perineum, lying to one side of the central raphe and in front of the anus, <sup>overlying</sup> the skin assumes the peculiar characteristics of the scrotum.

The external appearance of the scrotum varies with different circumstances. Under the influence of warmth, and in debilitated and old persons, it becomes elongated and flaccid; under the influence of cold, and in the young and robust, it is short, corrugated, and closely applied to the testes. ~~The ap-~~

The application of chemicals to the scrotum is attended by considerable pain, although these cause no discomfort to most other parts. It has an extensive surface, stands well away from the body, and is exceptionally well supplied with sudorific glands. The area around is equipped with coarse hair, similar to that of the axillae. The scrotal region, like the axillary, is a mammary region. KLAATSCH and BERRY HART have shown that the prepenial scrotum of the marsupials is the analogue and homologue of the mammary pouch of the female which primitively is the egg- or ovarian-pouch just as the scrotum is the testis-pouch. Whether the scrotum is developed prepenially; in the inguinal region as in the case of the rodents; or as a pendulous extension of the inguinal skin as in the human, - it is always developed in a mammary area. It is the homologue of the labia majora of the female, and upon a labium HARTUNG has recorded the occurrence of a definite mamma.

#### THE GUBERNACULUM and ITS ASSOCIATED STRUCTURES.

The developing testis is attached to the adjacent Wolffian body by a peritoneal fold, the mesorchium, and from the mesonephros a fold of peritoneum, called the inguinal fold, grows out to meet and fuse with another, the inguinal crest, which proliferates from the antero-lateral abdominal wall. A portion of the peritoneal cavity lateral to these fused folds is marked off as the future saccus vaginalis. During development the peritoneum of the inguinal fold forms two folds, one, the plica vascularis, ultimately conveys the spermatic vessels, the other,

the plica gubernatrix, contains the actively growing gubernaculum, the rudder or guide of the testis as it migrates towards the scrotum.

Up to the fourth month of intrauterine life the various layers of the abdominal wall are unbroken save for a fine strand of tissue which leads towards the site of the scrotum and evidently serves as a guide for the gubernacular outgrowth. But in this region of the abdominal wall SABIN and BERRY HART have demonstrated that there is a well defined line of lymph sinuses which are the starting point of lymphatic development for the skin of the anterior abdominal wall. In this region the body wall is not intact and a natural passage exists through which any organ escaping from the abdominal cavity will most easily make its way. It will be seen that this lymphatic distribution influences the line of growth of other structures.

In the third month the mesoblastic tissue in the lower end of the inguinal fold begins to pierce the abdominal wall external to the deep epigastric artery, the piercing force being obtained purely from the inertia of its own growth. The growing end, at first merely represented by fine strands of tissue, in later months increases in mass and carries over it and in front of it into the scrotal area a process of peritoneum and attenuated representatives of each stratum of the abdominal parietes.

In the fourth month the subperitoneal layer of non-striated muscular tissue in the inguinal fold and in the mesorchium takes on a rapid growth and at the same time the tissues of the entire abdominal wall undergo a localised evagination towards the scrotum. They are probably carried on by the growth

of the gubernacular bud which pushes its way to the scrotum, growing downwards as a solid fibro-muscular mass until it reaches the subcutaneous tissue which at that time completely fills the solid scrotum. The gubernaculum testis is an actively growing mass of fibro-muscular tissue which, starting from the muscular stratum in the mesorchium and inguinal fold in the inguinal fossa, invades the abdominal wall, every layer of which it carries as a prolongation within the scrotum. Upon the peritoneum thus drawn down the testis is dragged like a log upon a sledge.

The developing gubernaculum with the peritoneum and other representatives of the abdominal parietes forms the inguinal canal by a growth of its wedge-shaped end in the line of lymphatic tissue and lymph sinuses. The unstriated muscle radiates into the scrotum ahead of both peritoneum and striped muscle, and the unstriated muscle is the active penetrating agent. There is thus formed, prior to the passage of the testes through the abdominal wall, the inguinal canal. The canal is not formed by any mechanical dilating process connected with the migration of the testis; it is preformed by the penetrating growth of the gubernacular fibres along a definite lymphatic tract while the testes are still intra-abdominal.

The structures of the abdominal wall which are carried into the scrotum furnish the intercrural fascia, the cremaster, and the infundibuliform fascia.

The intercrural fascia is a thin membrane prolonged downwards around the surface of the cord and testis and is derived from the external oblique muscle. It is separated from the dartos by the layer of fat-free loose areolar tissue.



The cremaster is a musculo-membranous covering of the cord and testis derived from the internal oblique muscle. The purely muscular portion of this layer has the form of a series of loops, attached by one extremity to the inner end of Poupart's ligament, and by the other to the spine and crest of the pubis. The intermediate fibres form a series of successively lengthening loops which descend in front of the spermatic cord as low as the testis. The various loops are connected together by a membranous tissue.

The cremaster is a valuable supporting constituent in a pendulous organ and has a probable function in preventing dilatation of vessels in the cord and testes. Its action under voluntary impulses is well figured by WIEDERSHEIM. It has not been definitely demonstrated that the cremaster plays any direct part in the migration of the testis. It is the phylogenetic relic of the conus inguinalis (KLAATSCH) of rodents and insectivores, in which the transversalis and internal oblique muscle project into the inguinal fold to form a conical projecting eminence in the peritoneal cavity. In rodents this can be seen as a cone projecting into the abdomen from the scrotal site. Both KLAATSCH and WERTH figure a conus in the human embryo. WIEDERSHEIM states the opinion that these fibres of the transversalis and of the internal oblique must have grown into the fold. BERRY HART submits that these fibres cannot draw the testes into the scrotal pouch, for the direction of their fibres prevents this: nor can they draw the testes out; and that the periodic passage of the testes into and out of the abdominal cavity results by the growth, then the involution, and accommodation of the testes.



According to KINGSLEY, when the canal connecting the cavity of the scrotum (bursa inguinalis) remains open, as it does in marsupalia, bats, rodents, insectivores, etc., the descent is temporary, the testes being withdrawn into the peritoneal cavity at the close of the breeding season by the cremaster muscle, developed from the transverse abdominal muscle.

The cremaster does not exist in the testiconda, as the elephant, hyrax, seal, walrus, the cetaceans and monotremous mammalia; in these the testes are merely supported by their vessels and the mesorchium. The presence of the cremaster is always associated with a temporary passage of the testes from the abdomen, as in the rodents, insectivores, and bats, or with the permanent lodgment of the migrated testis in a scrotum.

The infundibuliform fascia is derived from the fascia transversalis of the abdomen, and becomes continuous with that structure at the internal abdominal ring.

The gubernaculum, as it grows through the abdominal wall, carries with it a process of peritoneum - the processus vaginalis. This in the human becomes occluded by adhesion or zygosis at two points soon after birth, though in a considerable proportion of individuals the process of closure is delayed. The upper point of occlusion is at the internal abdominal ring; the lower a short distance above the testis. That part of the processus vaginalis between the points of occlusion is known as the funicular process; the part surrounding the testis - the tunica vaginalis. In about 30 % of children the occlusion at the upper point does not occur until a considerable time after birth, and may even fail to appear altogether. Occlusion

may fail at the lower point likewise, or on the other hand, occlusion at the two points may occur normally, but the funicular process, instead of becoming obliterated, may remain patent and form a cyst. The processus vaginalis becomes obliterated in the marsupials; it is narrow in the Artiodactyla and Lemuroidea; wide open in the Perissodactyla; and in the Carnivora the beginning of its involution is seen.

"But this much is certain, that the closing of the mouth and neck of the sac is peculiar to the human species; and we must suppose the final intention to be the prevention of ruptures, to which men are so much more liable than beasts from their erect state of body." (JOHN HUNTER).

The chimpanzee, or African orang-utan, (*Simia Troglodytes*, Blum.), which of all mammalia approximates most closely to the human structure, resembles man in the early obliteration of the canal which leads from the peritoneal cavity to the tunica vaginalis. In the Indian (*Simia Satyrus* Linn.), on the contrary, the canal of communication is wide open. (OWEN. Foot-note to above).

MACKENZIE has called attention to the fact that the tunica vaginalis is the only serous membrane of the body which is supplied by cerebrospinal (sensation perceiving) nerves.

Other human peculiarities in this region are the unique form of Poupart's ligament which is scarcely developed in any other mammal; the width of the pelvis of the crural passage, and of the abdominal wall. All mammals adapted to the pronograde posture have a narrow pelvis and consequently have also a narrow anterior abdominal wall through which the inguinal canal passes very obliquely. The space between the edge of Poupart's ligament and the edge of the pelvis is much greater in

man than in any other animal, and the most internal part of this passage is left unfilled. The human method of walking and the great size of the head of the human fetus require a wide pelvis and the strong musculature of the abdominal parietes in contraction subjects the abdominal contents to considerable pressure.

In the course of the migration of the testis its mesorchium becomes shortened by the development of the gubernaculum, and the testis and epididymis become thus firmly bound by their posterior borders to the tunica vaginalis. After the testis is within the scrotum the gubernaculum undergoes involution, and in the adult only traces of it can be identified.

The migration of the testis in essence is as follows :

- The testis is united to a mammary area, supra-pubic, inguinal, perineal, or scrotal, at first by the inguinal fold and later by the gubernaculum, the canal-former, the guide, which is attached by its upper end to the Wolffian duct, the epididymis, and at the point where the globus minor and vas deferens meet, and by its lower end to the subcutaneous tissues in the groin, scrotum, pubis, and root of the penis. The developing gubernaculum, with the aid of the cremaster and peritoneum, forms a pit or fossa for the testis in the case of the rodents, and a more complete canal, or more or less pendulous scrotum in higher mammals, in whom the testes remain permanently lodged in the scrotum. The final situation of the testis is decided in great part by the relative development of the various fasciculi of the gubernacular fibres; in man the scrotal fibres are specially represented; in marsupalia - the pubic; in rodents and insectivores - the inguinal. KLAATSCH suggests that the changes induced by preg-

:nancy in the mamma are analogous to the changes in the conus inguinalis in the rutting male.

# THE UNDERLYING CAUSE of the MIGRATION.

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"What is the immediate cause of the descent from the loins to the scrotum? It is evident that it cannot be the compressive force of respiration; because the testis is commonly in the scrotum before the child has breathed, that is, the effect has been produced before the supposed cause has existed. In the testis pulled down by the cremaster muscle? I can hardly suppose that it is; because if that was the cause, I can see no reason why it should not take place in the hedgehog, as well as in other quadrupeds; and if the muscular testis had this power it could not bring it lower than the ring of the muscle."

"How far an erect position of the body and the effects produced upon the contents of the abdomen in breathing may contribute mechanically to the descent of the testicles when the natural operations of the animal economy have failed, I will not pretend to decide; but when we see these combined actions producing an unnatural descent of a portion of intestine, we may conceive that they are likewise capable of contributing to the descent of the testicle."

"The great length of the spermatic vessels in the adult will no doubt occasion a more languid circulation which, we may suppose, was the intention of nature". (JOHN HUNTER).

BERRY HART offers the following suggestions as to the possible causes. The Wolffian body in great part disappears and the testis naturally comes to occupy its position and so starts upon its migration. The developing inguinal canal grows so large as to surround the testis; the involuting gubernaculum does not seem to be an important factor; and disproportionate growth plays a considerable role. The cremaster does not cause descent by any means.

KINGSLEY on the other hand teaches that the change in the position of the testis is accomplished in part by the unequal growth of the body wall and the supporting ligaments. By the unequal growth of the gubernaculum and the body wall the testes are drawn down into the scrotum which is a protruding part of the body wall and into which a part of the coelom extends. This wall is formed in part from the genital folds which surround the genital orifice.

WIEDERSHEIM without hesitation teaches that the periodic withdrawal of the testis into the abdomen, in the case of the Rodentia and Insectivora, is accomplished by means of the cremaster muscle "a more suitable name for which would be the levator s. retractor testis."

EBERTH suggests that intra-abdominal pressure is a potent cause. BRAMANN considers that the distended sigmoid has some influence in depressing the left testis. Increased inclination of the pelvis has been considered to have an influence by altering the direction of the inguinal fold favourably for traction. The cremaster becoming lengthened has been supposed also to exert traction, while FRANKL regards the involuting gubernaculum as being responsible for the downward migration of the testis.

A not uncommon anomaly of the testicle is that in which the common mesentery, instead of becoming shortened and thus fixing the testicle and epididymis widely to the peritoneum, becomes narrow and elongated. Such testicles are usually arrested in their descent. The gubernaculum siezes and draws up only a loop of the vas deferens. This is due to the fact ~~that in such~~

that in such cases the inguinal fold, made up of two pieces,-a lower, ending on the vas deferens, and an upper, which continues the fold to the epididymis and testicle, - has not extended to the upper part of the inguinal fold.

WOODLAND has developed an argument which submits that the migration is the result of mechanical strains : -

"I hold that in the majority of the Mammalia, ( in which group descent has occurred), the testis attachment throughout the history of the race has been constantly subjected to severe strains consequent on the character and conditions of mammalian locomotion, and that on account of the resulting disruption or distention of the mesorchium, the testis has migrated in a postero-ventral line (i.e. in an opposite direction to the forward and upward accelerations imparted), coming to lie at the terminal periphery of the body wall and forming the scrotal protrusion."

He points out that in the case of the impulsively active mammals the period occupied by contact of the limbs with the earth is extremely brief and the height of the elevation considerable; and hence, though the angulation of the limbs tends to diminish concussion, the organisation is subject to the intense strains and stresses resulting from the enormous forces generated during locomotion. At each elevation of the body in mammals a considerable force is imparted to the organism as a whole (and by necessary implication to its constituent parts) in an upward and forward direction.

"If the constituent parts of the body be considered, it will be evident that such a force works differential effects among them. For these organs, largely differing among themselves in regard to mass, and the same force being incident on all, it follows that the individual reactions are different, and hence there exists a tendency to segregation of those organs of greater mass from those of lesser. Moreover, organs differ inter se in their relation to the rest of the body. If an organ be embedded or otherwise firmly attached to the main bulk, it will on account of its large area of attachment and close apposition readily share



both the elevations and depressions incurred in locomotion - the strains and stresses are distributed in time and space, and hence their intensity is lessened : if on the other hand, a massive organ be merely suspended from the main mass of the body, such a condition subjects the attachment to the influence of severe strains periodically recurring, the direction of which approaches that of the resultant acceleration of the trunk during its impulsive elevation."

The testis is a compact body of considerable density, it is suspended from the main mass of the body by a mesorchium, by its very nature it is apart from the rest of the body and its transposition is of no concern to the rest of the organism. There is no reason why they should not be segregated from the other organs.

According to KEITH : -

"There can be no doubt that in those mammals in which the testis leaves the abdomen it does so to escape the intra-abdominal pressure to which the abdominal viscera are subjected. Its descent is correlated with the evolution of the diaphragm and exclusion of the lungs from the abdominal cavity. Violent respiration and flexure of the trunk give rise to very high degrees of tension within the abdomen."

Reviewing the whole of the suggestions offered it would seem that not one but several causes have played their parts. WOODLAND's idea clearly explains the passage of the testis from the region of the kidney to the inguinal region of the abdomen, where it naturally comes to lie in the line of the lymphatic sinuses described by SABIN. A combination of mechanical strains and of high intra-abdominal pressure would then cause the testis to pass through the thickness of the abdominal wall and to lie against the integument of the inguinal region. Sudden and repeated rises of intra-abdominal pressure, and the irritation of the testis upon the overlying tissue causing thinning, would ultimately result in an evagination of the skin of



this region and so a scrotum would be formed. The irritation resulting from the movement of the testis would cause peritoneal adhesion and from such adhesions the inguinal fold could have had its origin.

And if the organism could adapt itself to function perfectly well under conditions in which in each generation the testis would almost invariably recapitulate the migratory process, being subjected to circumstances identical with those which produced the condition in its forebears, then what was once abnormality would become normal, variation would ultimately replace modification, and the mechanism of migration would ultimately become developed in anticipation of the descent.

"Originally, the descent of the testes did not occur until sexual maturity in all cases, but in many Mammalia (e.g. Marsupials, Ungulates, Carnivores, Primates), the process has gradually become shifted backwards ontogenetically to earlier periods, so that the formation of the scrotum takes place independently in the embryo in the form of the external genital folds." (WIEDERSHEIM).

So that in the impulsively active mammals, existing in media which do not negative the occurrence of accelerations of high degree, the process of migration which at first was repeated during the individual lifetime in consequence of the mechanical strains to which the testis was subjected, these resulting from violent locomotion and from the muscular action of the diaphragm and of the abdominal parieties, later became anticipated by the development of the gubernaculum, the guide of the testis through the lymph-tracks, and by the preformation of the inguinal canal.

In the case of fishes and birds there is no migration on the part of the testis. The most probable explanation of this is that suggested by WOODLAND, who submits that these animals exist in media which negative the occurrence of accelerations of high degree. Fishes are cold-blooded vertebrates which exist in a medium so similar in density to themselves that the force of gravity is not felt, while in the case of the birds the body is not entirely unsupported, the resistance of the air to the large ~~expanse~~ of body yielding considerable aid in this respect, and the small amount of self-sustainment needed can be provided by the minor elevations imparted by individual strokes of the wing. The reactions between the wing and the air are of necessity small, owing to the mobility of the latter substance, and hence, in spite of the great activity of birds, no great accelerations are imparted to the body - the locomotion is not impulsive.

Among the mammals, the Monotrema, Sirenia, Cetacea, most Edentata, Hyracoidea, Proboscoidea, and Phocidae, exist or have existed under conditions which negative the descent of the testis, and these conditions have either consisted in the absence of that type of terrestrial locomotion which has been the cause of the transposition of these organs, or of secondary factors which have either negatived the operation of the primary agency, or affected a reversion of the pre-existing effect of the same.

## THE RESULT of the MIGRATION.

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The testis which primitively functioned perfectly well when intra-abdominal left the abdominal cavity to pass into the scrotum where it performs its two functions : the production of spermatozoa and of an internal secretion, apparently just as well, if not better. It is too difficult to conceive that the migration to the scrotum has imparted any advantage to the organism, - a variation of this nature could not have been the raw material upon which natural selection worked. The process bears no great relation to either advantage or disadvantage, though it would seem that the scrotum is a physical disadvantage, for although it is protected to some extent by the thighs, yet the ease with which the scrotum is attacked and the devastating effects of contusions of the testes make a veritable Achilles's heel of this region.

Yet there seems to be no compensatory physiological advantage offering benefits which outweigh the physical disadvantage. The creatures with permanently abdominal testes flourish as do those whose testes are permanently scrotal. It would seem that the migration is but the inevitable concomitant of some other constant feature of the animal's existence, and has thus not arisen in relation to ulterior ends.

A study of the condition in which the testis fails to complete its migration will show that the result of the migration has been that the testis which functions when within a scrotum is incapable of producing spermatozoa whilst within the abdominal cavity. Throughout the centuries the testis has become so adapted to function under the conditions which exist in the scrotum that it can no longer do so in other situations. This would indicate, therefore, that the conditions which are present within the scrotum are not those of the interior of the abdominal cavity.

#### CRYPTORCHISM.

"The descent of that testicle is very slow which is not complete before birth, often requiring years for that purpose; and it sometimes never reaches the scrotum, especially the lower part of it. There is oftener, I believe, an inequality in the situation of the two testicles than is commonly imagined; and I am of the opinion that the lowest is the more vigorous, having taken the lead readily, and come to its place at once."

"It is not easy to ascertain the cause of this failure in the descent of the testicle; but I am inclined to suspect that the fault originates in the testicles themselves. This, however, is certain, that the testicle which has completed its descent is the largest, which is more evident in the quadruped than in the human subject; as in these we can have an opportunity of examining the parts when we please, and can determine how small in comparison with the other that testicle is which has exceeded the usual time of coming down; it never descends so low as the other.

"When one or both testicles remain through life in the belly, I believe that they are exceedingly imperfect, and probably incapable of performing their natural function, and that this imperfection prevents the disposition for descent from taking place." (JOHN HUNTER).

In connection with the last paragraph it is of interest to note that in Palmer's edition of JOHN HUNTER's Works, OWEN adds the following footnote : -

"It seems remarkable, that with this experience Mr. HUNTER should have formed, from inconclusive analogy, and promulgated an opinion tending to occasion so much unhappiness as that which attributes exceeding imperfection, and probable incapacity of performing their natural functions, to testes which in the human subject are retained within the abdomen. That there is nothing in such a situation which necessarily tends to impair their efficiency, is evident from the number of animals in which they constantly form part of the abdominal viscera. And in those in which the testes naturally pass into a scrotum, their continuance in the abdomen, according to our author's own observation, is accompanied only with a difference of size or shape; now we may readily suppose that this may influence the quantity, but not necessarily the quality of the secretion."

Today we know that HUNTER was infinitely nearer the truth than was his editor.

Cases of arrested migration have occurred in such numbers that it has become clear that the testis may become arrested at any point in the migration from the primitive position to the fundus of the scrotum. It may be retained within the abdominal cavity in any situation between the primitive position and the inguinal region; within the inguinal canal; or, having traversed the canal, remain just below the external abdominal ring; or it may reach the scrotum but hang at a higher level than normal. In these cases a certain amount of mobility of the testis is generally present: thus a testis which may be occasionally palpable in the inguinal canal, at other times will be found to have disappeared into the abdominal cavity, or on the other hand, it may have left the canal and entered the scrotum.

Such indefinite retention within the abdominal cavity or within the inguinal canal of one or both testes is termed cryptorchism.

Many cases of cryptorchism are recorded in the medical and veterinary literature. It has been described as occurring in the dog, the pig, the bull, the stallion, and in man, and is sufficiently common that every surgeon has met with it in the course of his practice and is familiar with its treatment. Cryptorchism may be regarded as a phylogenetic reminiscence of the situation of the testes in other groups.

In cases of cryptorchism the tunica vaginalis is always present and is often remarkably large and baggy, sometimes fully occupying the scrotum while the testis itself is arrested in the inguinal canal. This agrees with the mode of development, for the processus vaginalis is neither pushed down by the testis, nor pulled down by the gubernaculum, but is an outgrowth of the peritoneum. In the great majority of cases the processus is not obliterated and hence hernia is a common complication in man. The epididymis is generally small, ill-developed, and loosely connected with the body of the testis, and the mesorchium is often unduly long. The scrotum is often only imperfectly formed when the condition is unilateral, and when it is bilateral the scrotum may be represented merely by an area of corrugated skin.

The testis itself is generally smaller than the normally placed organ and is softer to the touch. When it lies within the inguinal canal there is an increased size of the internal ring and a laxity and thinning out of the fibres of the internal oblique. Usually the external ring is also stretched. In those cases in which the testis has never entered the canal

and in which there is no hernia of the intestine the ring may be small and ill-developed.

"Arrest of descent is commonly regarded as a symptom of arrest of testicular development. JOHN HUNTER regarded arrested descent of the testicle as due to an imperfection in its development; all recent observations support his opinion." (KEITH).

"It is commonly believed that the imperfection of an undescended testicle is due to its failure to reach the scrotum. This I believe to be an error. An undescended testis fails to reach the scrotum because of its imperfection." (BLAND SUTTON).

The opinion of JOHN HUNTER, endorsed by such authorities as KEITH and BLAND SUTTON, is indeed a weighty one; so much so, that it would seem impertinent to question its truth. But perhaps when HUNTER used the word "imperfection" he meant to include imperfection in the development not only of the testis, which after all plays but a passive rôle in the process of its migration, but also imperfection in the development of the local peritoneum, the gubernaculum and its associated structures, and of the inguinal canal.

Let us take an example. The long mesorchium may allow the testis to hang so freely in the abdominal cavity that it may fail to enter the canal; there may be deficiency of the muscular action of the gubernaculum, or abnormality of its upper attachment, so that the normal pull and guidance may be lacking; intra-uterine peritonitis may have caused adhesions which limit the mobility of the testis; shortness of the vas deferens and of the blood-vessels, though more likely to be an effect, may also be a cause of non-descent; the inguinal canal may be ill-formed or the scrotum ill-developed, so that descent



is impossible. Overaction of the cremaster may be another possible cause, for in infant and children strong action of this muscle may occasionally draw the testicles up even beyond the external ring. It is well known that in childhood the cremasteric reflex is very active, and the testis is apt to be drawn up so as to enter the inguinal canal; among human beings, however, cases, in which the testis periodically enters the abdomen, remains there for a space, and then appears again, are very rare. Such a case is reported by MURARD. A boy, 16 years old, had suffered for many years from occasional violent pains; at the age of 13 these were found to coincide with the sudden disappearance of the left testis, which would remain inside the abdomen for five days until another violent, almost anginal, pain announced its return. These sudden disappearances occurred every month, but when MURARD examined the boy the testis had been absent for 15 days. At operation an open vaginal process was found, but the testis could not be felt through the ring. Traction on the cord, however, brought it to view, and it was easily replaced and anchored in the scrotum. The epididymis was absent, the vas ending blindly.

Imperfection of the testis most surely can be a cause of its non-descent, but it is certain that this is not the sole cause, for though a testis is of such a nature that it is capable of passing into the scrotum, yet it is a passenger and depends on other agents for its travel. Unless it is of such a size and shape that it cannot be conveyed to the scrotum, then its non-descent is the result of imperfection not of the testis but of the structures and forces to which the migration is due.



ECTOPY.

In certain cases the testis passes through the inguinal canal but instead of entering the scrotum reaches some abnormal situation, some ectopic position which is again a phylogenetic reminiscence of the situation of the testes in some other group. It may pass upwards and outwards towards the anterior spine of the ilium; it may pass inwards in from the pubis to the root of the penis; it may pass backwards into the perineum; or it may pass downwards and outwards into Scarpa's triangle.

Many cases of ectopy are recorded in the literature, and it is met with in all mammals.

"The testicle, in changing its situation, does not always preserve a proper course towards the scrotum, there being instances of its taking another direction and descending into the perineum. How this is brought about it is difficult to say; it may possibly be occasioned by something unusual in the construction of the scrotum; or, more probably, by a peculiarity of the perineum itself; for it is not easy to imagine how the testicle could make its way to the parts about the perineum if these were in a perfectly natural state." (JOHN HUNTER).

A review of the recorded cases of ectopy shows that the testis in these cases has come to lie in a position which is characteristic of that of the testis in other group. The cause, which can be verified by operation, is that there exists some abnormality of the insertion of the gubernaculum. In the case of the human, the scrotal fibres of insertion are most strongly represented and the testis normally passes into the scrotum; in marsupials, the pubic fasciculi are the best developed and the testis passes into a prepenial pouch, and so on. So that if some fasciculus other than the usual is relatively overdeveloped then its action will be to guide the testis into

an abnormal situation. The insertions of the gubernaculum are as follows : into the muscles along the course of the inguinal canal, into the pubis and root of the penis, into the region of Scarpa's triangle, and into the perineum where the fibres are attached to the ramus and to the tuberosity of the ischium.

Other explanations of ectopy are that the gubernaculum, making its way towards the scrotum, took an eccentric course and secured abnormal insertions, or that the testis may be displaced to an unusual position by the pressure of a co-existing hernia.

#### THE EFFECT on the TESTIS of NON-DESCENT.

"It is certain that in the majority of cases the imperfectly or abnormally descended testicle is functionless, at any rate as regards spermatogenesis. But though the function of spermatogenesis is absent, that of producing the internal secretion necessary for the development of the secondary sexual characters of the male is generally, but not always, carried out. That the function of spermatogenesis is lost is shown by the fact that such persons are unable to beget offspring and is also confirmed by the histological examination of retained testes after removal.

"In rare cases the spermatogenetic function is not lost, even when there is a double imperfect descent with very small testes, or when both organs are arrested within the abdominal cavity; this has been proved both by the presence of normal tubules and active spermatozoa, and also by the fact that these persons have proved capable of procreation. Many examples of this are recorded in medical literature. There is, however, evidence that those in which spermatogenesis is normally carried out are young men mostly under thirty years of age. In men over this age the imperfectly descended testis is nearly always functionless. In the majority of cases under thirty the spermatogenetic function is absent and the proportion of functional organs is probably small." (TURNER).

"After careful observations extending over many years I only once found spermatozoa in an undescended testis." (BLAND SUTTON).

"It is not rare to find spermatozoa in testicles which have remained in the lower part of the inguinal canal, but in those in the upper part, and in those taken from the abdomen, this is exceptional. (HOB DAY).

M'FADYEAN who examined 25 cryptorchids for HOB DAY found that of 14 from the abdominal cavity only 2 contained spermatozoa, and of 11 from the inguinal canal - 3 from the upper portion - only 5 were capable of functioning. GURLIT failed to find spermatozoa in testes from the abdomen; DOLLAR states the opinion that such testes contain either degenerated spermatozoa or none at all; WESCHE found that testes within the inguinal canal were capable of producing functional sperms, while PAUCOUÉ records the case of a stallion in which both testicles were undescended yet who sired many colts of which five suffered from the same condition.

"As a rule misplaced testes are undersized and when removed from the adult they show degeneration and atrophy of the secreting structures. In one undescended testicle which we removed from a man 45 years old in the course of a radical operation for strangulated hernia, microscopical examination of the gland, which was about the size normally found in a child of twelve, showed it to be fully functional, although it had been subject to a number of inflammatory attacks. When testes fail to descend, as a rule they are incapable of producing spermatozoa. True atrophy nearly always is observed in cases of non-descent and ectopy." (WHITE and MARTIN).

The condition of the testis in these case is very similar to that caused by vasectomy or exposure to X-rays :-

"Vasectomy involves either cutting the vasa deferentia in such a way that the cut ends do not reunite. In consequence of the closure of the outlet of the testis the germinal cells slowly degenerate, and finally completely disappear. How such an effect is produced we do not know. That this result does take place is borne out by the unanimous testimony of all those who have successfully performed the operation. ANCEL and BOUIN showed (1903) that breaking the continuity of the vas deferens suppressed

spermatogenesis in 8 to 12 months. Both the Sertoli cells (the nourishing cells of the germinal epithelium) and the interstitial cells persist. Such animals remain sexually active and their secondary sexual characters are not affected. MARSHALL states that in the hedgehog the remarkable periodic enlargement of the testis takes place even after vasectomy, although the germ-cells have disappeared."

"In mammals the testes fail at times to pass through the inguinal canal, and, in consequence of their retention in the body-cavity, the germ-cells fail to develop. On the other hand, the interstitial cells of the testis develop normally. Cryptorchid individuals show the normal secondary sexual characters of their species. How retention of the sperm should give rise to the same result as cutting the duct, viz, absorption of the germinal cells, is not known. A possible solution may be found in the pressure exerted on the testes, both when retained in the abdomen and when their outlets are stopped by tying or cutting the ducts.

"Finally it has been long known that continued or repeated exposure to X-rays or to radium causes the destruction of the germ-cells, but leaves the interstitial cells intact and presumably functional. Destruction of the germ-cells by X-rays has no effect on the secondary sexual characters.

"This threefold evidence demonstrates that in the male of the mammalia most, perhaps all, of the secondary sexual characters that are affected by castration are not affected by the destruction of the germ-cells. This conclusion supports very strongly the view that the interstitial cells are the cellular element in the testes that influence through internal secretion the development of the secondary sexual characters of the male." (MORGAN).

The above extracts represent the experience of British surgeons. It is certain that if both testes are ectopic, or if there has been non-descent of both, then in the great majority of cases spermatogenesis is entirely absent, and the individual is aspermatic and incapable of reproducing his species, although the internal secretion of the testis is exhibited and the individual has the secondary sexual characters of the male. Further, the individual experiences sexual desire, sometimes in an aggravated form, so that this desire and the behaviour consequent upon it do not depend upon the presence of spermatogenesis.

If but one testis is retained or ectopic then the other

normally placed one is sufficient for the purpose of reproduction, but if, as in the case of the domesticated animals, this normal testis is removed and the retained or ectopic one left behind, the animal - a rig - still is not a castrate but exhibits sexual desire and is frequently a source of great nuisance and danger in the stock-yard. However, some writers maintain that behaviour alone is not a reliable indication of the presence or absence of the testes, since rigs sometimes behave like geldings and geldings - like stallions.

In exceptional cases the abnormally placed testes can and do produce functional spermatozoa. It is seen that the nearer the misplaced testis is to the scrotum the more likely the chances are that it will be found to be capable of producing functional spermatozoa. It is not rare to find spermatogenesis in a testis retained within the lower portion of the inguinal canal, but a testis lying for an indefinite period towards the upper end of the canal is commonly aspermatic, and testes retained within the abdominal cavity are only very exceptionally spermatogenic.

In the case of the rat, the testis is spermatogenic only when fully descended, when returned to the abdominal cavity spermatogenesis is in abeyance. GRIFFITHS in an experimental investigation on dogs found that although the testes placed within the abdominal cavity developed normally up to the time of puberty, they never produced spermatozoa, and when the testes of grown dogs were returned by surgical measures to the abdominal cavity they invariably atrophied and never remained functional.



McADAM ECCLES thus describes the histological structure of the typical retained testis : -

"The seminiferous tubules, or what should be seminiferous, are smaller, more widely separated from one another by the interstitial tissue and are fewer in number, and probably shorter in length, than those of the normal organ. Between the tubules themselves there is much loose connective tissue which is rich in blood-vessels, in spite of the otherwise ill-development of the gland. Scattered throughout this tissue there are nuclei, belonging almost certainly to peculiar interstitial stroma cells. In some sections these appear to have undergone considerable development, both in number and in size. The basement membrane of the abortive tubules is well developed, but the lumen is filled with a mass of granular debris, containing a large number of nuclei of various shapes and sizes, these being probably derived from the cells lining the tubule. Neither spermatoblasts nor spermatozoa can be demonstrated in the tubules of by far the larger number of imperfectly descended testes."

MICHON and PORTE record their examination of six undescended testes removed at operation. The ages of the patients ranged from 14 - 26 years, all save one having reached puberty. There were clear signs of spermatogenesis in one case, and possibly in one other; in the remaining four it was absent, section showing pre-pubertal appearance (ages 14, 16, 17 and 26 years). The tubules appear to be narrower in the absence of spermatogenesis. The interstitial cells become more abundant as age advances. When few, they form little groups of three to eight cells; when many they form little islets of some size. These cells may even form little glands - the "para-epithelial masses" of HANSEMAN and others. The authors believe that a quantity of inter-tubular fat is evidence of degenerative processes; there was but little in the testes showing signs of spermatogenesis.

Any mal-position of the testis leads to degenerative changes, accompanied by atrophy and loss of function. The mal-placed testis is more prone to injury and to repeated attacks of inflammation, this being due, most probably, to the fact that in its abnormal position the testis is less mobile. The retained testis is often the seat of cystic degeneration and not infrequently of neoplasms, benign and malignant.

RUSSELL HOWARD records that in 57 cases of malignant disease of the testis, in 9 the affected organ was imperfectly descended. A recent study made by the present writer shows that in the horse, a testis retained within the abdomen is almost invariably the seat of tumour growth which, in the case of two-year olds at any rate, is benign in nature, while a testis retained within the inguinal canal, if abnormal, is merely aspermatic.

It can be accepted as a rule that the nearer to the normal position the testis lies, the more likely it is that spermatogenesis will be complete and the less likely that the testis will become the seat of tumour growth.

If the scrotum is the normal situation of the testis then the environment is such that the undue activities of the other component tissues of the gonad are regulated and held in check by the dominating activity of the actual germ-cells. But in an abnormal situation the conditions are such that spermatogenesis is embarrassed and the other less delicate tissues are permitted to proliferate exceedingly.

THE RELATION between IMPERFECT DESCENT and ABSENCE  
of SPERMATOGENESIS.

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"The relation between imperfect descent and imperfect development of the testis with absence of its chief function is a question of great interest and still is a matter of uncertainty!" (TURNER).

There are two possible explanations of the undoubted correlation. One is that imperfect development of the testis is the cause of its non-descent, the other that the testis is imperfect because of its non-descent.

In the first case there may be associated with the condition which leads to imperfect descent some abnormality of, or reacting upon, the germinal epithelium which prevents the normal growth and development. In these circumstances, in the face of such developmental abnormality, no treatment at any time would be likely to restore the spermatogenic function. In the second, full growth and functional development are possible and do indeed take place up to the time of puberty, but at this period, when the final stages should take place, the abnormal situation of the testicle in some way interferes with this and atrophy soon follows; or, as does happen in rare cases, the testis continues its functional development beyond puberty and actually produces functional spermatozoa, but recurrent attacks of inflammation and



other pathological processes which are particularly likely to occur in any mal-position, lead to degenerative changes, accompanied by atrophy, tumour-growth, and loss of function.

If there is no irreparable developmental abnormality of the testis and the absence of the spermatogenic function results from the mal-position, then obviously if, before degeneration has occurred, the testis is placed in its normal situation in the scrotum the essential function of the testis should appear in due course.

The fact that the operation of Orchidopexy is the recognised treatment of undescended testis is an indication that the surgeon actually hopes with reason that the transplanted testicle will so recover that the spermatogenic function will be restored. The surgical teaching briefly is as follows :

When the malposition is unilateral and the normally placed organ shows no sign of arrested development, the undescended testis should be transferred to the scrotum, or if the transplantation is difficult, the testis being much atrophied or the cord being short, the testis should be excised. The remaining testis can function sufficiently well. When both testes are imperfectly descended neither should be excised and the ideal treatment again is transplantation to the scrotum. If this is found to be impracticable, they are returned to the abdominal cavity. The operation, if it is to be attended by any great hope of success, should be performed before puberty.

Orchidopexy is frequently a failure and the disappointing results are mainly due to the following conditions which

defeat the intention of the operator to secure the uninjured testis into the scrotum, such as: injury to the testicular tissues, interference with the trophic supply of the testis, injury to the vas, post-operative persistence of fascial or gubernacular bands, and an undeveloped scrotum. These causes of non-success are not testicular conditions, and TURNER's method of treatment in which he transplants the testis through the septum to the opposite side of the scrotum offers a means of obviating the above causes of failure.

It may be accepted that when an immature testis is secured within the scrotum without operative injury, it will complete its development and function normally. The later in life the operation is performed, the less chance there is that the testis will assume a functional capacity.

If this is so, then the spermatogenic function occurs in one situation - the scrotum, and not in another - the abdominal cavity, in those mammals in which the descent of the testis is a normal process. The differences in the conditions which obtain in the two situations are responsible for the presence and the absence of the function of spermatogenesis.

After much thought and experimentation it became clear that the great difference between the two situations was a matter of temperature.

THE RELATION of EXTERNAL TEMPERATURE and the REPRODUCTIVE  
FUNCTION.

"Animals have their natural feelings raised or increased according to the perfection of the parts connected with such feelings, and the disposition for action is also in proportion to the state of the parts and the excitements of such feelings. But, that these feelings may be duly excited, it is necessary that the animal and the parts should be healthy, in good condition, and in a certain degree of warmth suitable to that class to which the animal belongs. In the greatest part of the globe there is a difference of warmth of the same district at different periods, constituting the seasons; and the cold in some of them is so considerable as to prevent those feelings or dispositions in animals from taking place, and to render them, for the time, unfit for the purpose of generation. This is owing to the testicles becoming at this season small, and therefore unfit to give such dispositions, as in the case of very young animals. This fact is very obvious in birds, of which the sparrow may be produced as a proof. For if a cock-sparrow is killed in the winter, before the days have begun to lengthen, the testicle will be found to be very small; but if that organ is examined at different times in other sparrows, as the warmth of the weather increases, and if the examination is continued to the breeding-season, the difference in size of the testicle will be very striking. This circumstance is not peculiar to birds, but is common; as far as I yet know, to all animals which have their season of copulation. In the buck we find the testicles are reduced to a very small size in the winter; and in the land-mouse, mole, etc., this diminution is still more remarkable. Animals, on the contrary, which are not in a state of nature have no such change taking place in their testicles; and not being much affected by seasons, are consequently always in good condition, or in a state to which other animals that are left to themselves can only attain in the warmer season. Therefore, in man, who is in the state we have last described, the testicles are nearly of the same size in winter as in summer; and nearly, though not exactly, the same thing may be observed in the horse, ram, etc., these animals having their seasons in a certain degree. (JOHN HUNTER)

There is considerable evidence which goes to show that spawning in the sea and in fresh water, and also in terrestrial conditions, is regulated by temperature. C. L. TURNER in his paper "The Seasonal Cycle in the Spermary of the Perch"

has shown that the beginning of the annual decline in temperature is contemporaneous with the seasonal volumetric increase in the testes, and that the beginning of the seasonal decrease in the testes is contemporaneous with the beginning of the seasonal rise in the temperature.

"Many examples could be quoted to demonstrate that the rule is for a species to spawn earlier and to develop more quickly in warm water: that, in other words, the period of spawning is early in tropical seas and conditions, and later to the north and south of the tropical belt, and that the period of growth is increased with lowering of temperature"

"In the case of the Protista and the Metazoa which reproduce rapidly, an annual phase may be postulated which closely follows the rise and fall of temperature."

"There are aquatic and terrestrial species which in one situation reproduce once a year, and in warm seasons or in warmer situations reproduce twice a year."

"It may be granted therefore that growth and reproduction vary in length and periodicity with temperature."

"There may be said to be three phases of life in all animals: immaturity, maturity, and spawning. If the act of spawning is not followed by death, then there succeeds a series of similar phases. If we are prepared to recognise that the phase of immaturity is not ended alone by the attainment of the requisite somatic growth, then it is regulated by an organ which acts as an inhibitor of the next phase, and continues to act, not merely until the soma is in the requisite condition, but until the environment is also favourable. Such an organ must be placed in a convenient situation for receiving impressions from the environment and for communicating to the blood a hormone the function of which is to inhibit the development of the gonad."

"In the case of the aquatic animals we naturally turn to the gills to see if such an organ is provided, and it is already apparent that the thymus has been developed for this purpose. The thymus is a larval organ which develops in association with the gills, and it is already known that its secretion inhibits the growth of the gonads. In the Craniata the thymus is removed from its primitive position in the gills, but it lies near the gills in fishes, and in them and the higher Craniata it continues to exercise its function of controlling the period of adolescence. When the thymus ceases to supply its secretion to the blood the gonad commences its period of growth, and it is probable then that the thyroid comes into action to control in similar manner the growth of the gonad. We can imagine the thyroid controlling the degree of growth until temperature and other conditions are favourable for spawning. The gonad itself during the period of growth contributes messages to the blood which influence growth and produce migrations."

"With these organs we have to associate the pituitary, and the parathyroids. The former appears to be very like the thyroid in function, and the latter are yet little understood."

"The action of such organs of the environment may tend to be automatic, as has been suggested, but it is probable that direct impulses are introduced producing adaptation to changes in salinity and temperature."

"We have yet a lot to learn from biochemical inquiry and from experiment as to these fascinating ductless glands. I have in the meantime, tried to show that some of them are concerned in conveying impressions of the environment to the soma and to the germ-cells by a series of impulses carried by the blood, and leading to a primitive but effective internal and external integration. It is probable that reproduction in general in Protozoa, and in the cell as in Metazoa, is so controlled, and that such functional effects may have a profound pathological bearing." (Meek.)

F. H. A. MARSHALL has collected considerable evidence which supports the contention that reproductive activity and external temperature are intimately correlated. He cites the work of ANNANDALE, ASHWORTH, CHILD, REAMUR, SEMPER, GRAHAM KERR, BLES, and SPALLANZANI, and brings forward many new facts which corroborate the conclusions of these investigators. Doubtless other factors are concerned in the regulation of reproductive activity; it is sufficient for the moment to recognise that external temperature itself is a potent factor.

The suggestion is that there is an optimum temperature at which spermatogenesis is best effected or that the testis has become adapted to function best at a certain temperature.

The normal body temperature is the resultant of two factors : thermogenesis, the development of heat within the body mainly by muscular action, voluntary and involuntary; and thermolysis, the loss of heat from the body, the most important factor in which is the temperature of the environment.

In the warm-blooded animals these two factors are usually so nearly equal that the resulting temperature does not vary



materially. But the temperature of the body is not the same throughout. JOHN HUNTER gives an account of certain of his experiments as follows :

"Experiment II. I introduced the ball of my thermometer into the urethra about an inch; which having remained there about a minute, the quicksilver rose to  $92^{\circ}$ ; at two inches it rose to  $95^{\circ}$ ; at four inches to  $94^{\circ}$ ; and when the ball had got as far as the bulb of the urethra, where it was surrounded by warm parts, the quicksilver rose to  $97^{\circ}$ .

Experiment 20. On a healthy dog. The ball of the thermometer being introduced two inches within the rectum, the quicksilver rose to  $100\frac{1}{2}^{\circ}$ . The chest of the dog was then opened and a wound made into the right ventricle of the heart; and immediately on the ball being introduced, the quicksilver rose to  $101^{\circ}$  exactly. A wound next was made some way into the substance of the liver, and the ball being introduced, the quicksilver rose to  $100\frac{3}{4}^{\circ}$ . It was next introduced into the cavity of the stomach, where it stood exactly at  $101^{\circ}$ .

From these experiments on mice and upon the dog, it plainly appears that every part of an animal is not of the same degree of heat; and hence we may reasonably infer that the heat of the vital parts of man is greater than either the mouth, rectum, or the urethra." (On Animals producing Heat, p.131.)

The accurate measurement of the temperature of the surface of the body presents many difficulties, but  $32^{\circ}\text{C.}$  has been accepted as a standard and is probably not far from the true value. The temperature inside the body on the other hand, is known to be not far from  $37^{\circ}\text{C.}$  So that there is a temperature gradient of  $5^{\circ}\text{C.}$  indicating a very appreciable difference between the temperature of the deep and of the superficial parts.

BENEDICT and SLACK have shown that the temperature rises with the depth to which the thermometer is inserted until at 6 - 8 cms. a constant temperature is reached, and that up to this depth the temperature gradually rises from that of the body-surface to that of the interior. They also demonstrate that there is a tendency towards parallelism between the temperature of the different parts of the body.

It follows that a testis within a scrotum, or sub-integumental in the inguinal or perineal region, or even within the inguinal canal, is not subjected to the same temperature as the testis retained within the abdominal cavity.

Moreover, reference to the structure of the scrotum shows that this area of modified skin with its dartos tunic provides the testes with as thin a covering as any protected organ can possess. It is also excellently equipped for the purposes of heat regulation. The skin is well supplied with sudorific glands and the area is one where transpiration is peculiarly active. The subcutaneous tissue is free from fat, and so possesses no insulating, no heat-retaining property. Under the influence of external cold the dartos corrugates the skin so that pockets of warmed air hinder further heat-loss; under the influence of external warmth, the scrotum becomes flaccid so as to expose every bit of its surface in order to increase heat-loss locally. The scrotum stands well away from the body and is thoroughly exposed to the varying degrees of external temperature. The scrotum is a specialised area of the body-surface in which the mechanism for local heat-loss has become especially developed. The reactions to heat and cold show that the scrotum is possessed of an efficient heat-regulation mechanism.

The testis which functions perfectly when in the scrotum does not function, so far as spermatogenesis is concerned, when within the abdominal cavity. But in those animals in which migration does not occur, the testis functions perfectly well within the abdominal cavity and an area of skin equivalent to the scrotum cannot be experimentally reproduced.



It follows that the testis which originally was abdominal in position but which is now scrotal has become so adapted to function completely in this new situation that it can no longer carry out its functions when retained within the abdominal cavity and also, maybe, that some accessory mechanism which regulated the functioning of the abdominal testis has become lost in consequence of the migration of the testis to the scrotum which possesses an efficient temperature-regulating mechanism of its own.

It has been shown that a scrotal testis replaced within the abdomen becomes aspermatic and that the operation of Orchidopexy results in the aspermatic testis becoming spermatic. In the old and debilitated the scrotum is flaccid and unresponsive to changes in the external temperature and in these cases the powers of reproduction are much lessened. In such diseases as Elephantiasis arabum, in which the scrotal integument becomes much thickened and inelastic, the testes become atrophic. The scrotum in these cases becomes so altered in structure that its essential qualities are destroyed; the testes within such a scrotum are therefore not permitted to function normally.

Mechanical forces caused the migration of the testis from the primitive position to the terminal periphery so that it naturally came to lie immediately beneath the parietes in the inguinal region. In this situation the temperature is distinctly lower than that about the primitive position and the testis would become adapted to function completely in a situation in which the external stimuli could be appreciated directly. The accessory mechanism through which the environmental stimuli formerly and indirectly affected the organ would come to be less and less delicate as it became less necessary.

Meanwhile increasing impulsiveness of action would be developed and with it increased intra-abdominal pressure. The testis would be forced along the line of lymph-sinuses and come to lie immediately beneath the inguinal skin. But here it would be exposed to injury because of its slight mobility and flexion of the thigh upon the abdomen. Ultimately a hernia would be produced and into the scrotum so formed the testis would pass, becoming thus secure from injury yet retaining all the advantages of a sub-integumental position.

The testis was forced to pass to the terminal periphery: it was forced to pass into a herniated sac. But it has become so adapted to function in this situation that it can no longer do so when retained within the abdomen. The process has been of the nature of an adaptation by which the harmful results of a partial migration have been turned to advantage. The testis has come to lie in a situation in which the appreciation of external conditions is locally so complete that there is no longer any need for such a mechanism as that of the pharyngeal derivatives.

It is an established fact that in the mammals in which the testes normally pass into a scrotum the thymus atrophies and almost completely disappears about the time of puberty. In the testiconda, so far as records are available, it appears that the thymus persists throughout the animal's lifetime. But it is certain that the thymus atrophies in the female mammal and in birds and in these the gonad does not pass into a scrotum.

Nevertheless it is possible that in the testiconda the incidence of spermatogenesis is governed by the activities of the thymus - or of some other of the pharyngeal derivatives - which is so situated that it can readily appreciate the seasonal

changes of external temperature, whereas in the case of the higher mammals the function of this gland of internal secretion has become restricted to that of inhibiting the too rapid functional development of the testis up to the time of puberty, by which time the body is sufficiently grown to entertain the physiologically expensive demands of spermatogenesis.

The fact that spermatogenesis in many of the mammals and birds is not restricted to a particular season but is practically continuous throughout the year is to be explained as the direct result of domestication with its plentiful food, artificial warmth, and overstimulation of the reproductive system.

In the female the developing gubernaculum secures attachments to the uterine wall. The ovary has not been forced to the terminal periphery and there has been no adaptation.

The testes of Pisces, Amphibia, Reptilia, and of Aves do not pass to the periphery and there has been no adaptation.

The testes of Rodents, Insectivores, and Bats, pass periodically into a sessile scrotum and after the breeding period return to the abdominal cavity. When they are within the scrotum they are large and spermatid, when they are within the abdominal cavity they are shrunken and aspermatic. They can return readily to the abdomen since at the end of the period of reproductive activity they are much shrunken and the processus vaginalis is patent. This mechanism is an adaptation which in these groups is perfectly satisfactory and their reproductive activities are restricted to the times during which the testes are down within the scrotum.

18.

In the case of the testicondā the testes do not pass far from the primitive position. If they do pass to the inguinal region they still lie deep and they are capable of functioning in a surrounding temperature which is that of the general abdominal cavity. There has been no adaptation since there has been no migration of any magnitude.

#### SUMMARY.

1. The mechanism of the migration of the testis is considered and a suggestion as to the underlying cause is made.
2. The results of the migration, as illustrated by the records of experimental surgery and by the condition of the testis in cases of cryptorchism and of ectopy, are examined.
- 3 The relation between imperfect descent and imperfect functioning of the testis is considered and an effort made to show that, contrary to the opinion of recognised authorities, the imperfection may be the result and not the cause of the imperfect descent.
4. In support of this, an investigation as to the exact differences between the conditions within the abdomen and those within the scrotum is made. The obvious difference was found to be a matter of temperature. There is a difference of about 4 C.
5. It is suggested that in certain groups the testis which has passed from the primitive position has, through time, come to function best at a temperature which is very different from that within the abdominal cavity. This is offered in explanation of the aspermatic condition of undescended testes.
6. The relation between external temperature and reproductive activity is discussed. It is shown that this relationship is

an intimate one. It is suggested that in those animals in which the testes remain permanently within the abdominal cavity, their functional activity is controlled by some such gland of internal secretion as the thymus, whereas in those animals in which the testes migrate to a scrotal position where local heat-regulation is very efficiently performed, the thymus, being no longer required, atrophies about the time of puberty.

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